# CAPTIVE OBSERVATIONS ON MATING, STRIDULATION AND MALE GENITAL BRUSHES OF THE AUSTRALIAN FLOWER CHAFER *PHYLLOPODIUM PALMATUM* (SCHAUM, 1848) (COLEOPTERA: SCARABAEIDAE: CETONIINAE)

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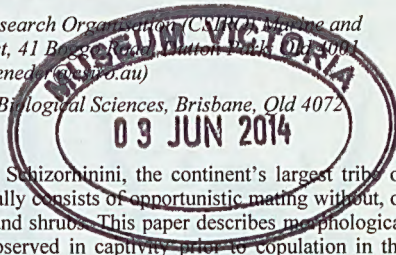
Abstract

Mating behaviour in the majority of Australian Schizorhinini, the continent's largest tribe of Cetoniinae, varies little among species and generally consists of opportunistic mating without, or with minimal, courtship on the flowers of trees and shrubs. This paper describes morphological features and courtship and mating behaviour observed in captivity prior to copulation in the atypical Schizorhinini species *Phyllopodium palmatum* (Schaum, 1848). Stridulation is produced metasternal-sternitaly, a method not described previously in Australian Cetoniinae, which was observed during courtship and in behaviour assumed to be defensive. Both sexes engaged in apparently stimulatory behaviour in courtship. The female was observed to bury into soil during mating, a behaviour possibly associated with avoiding predation. For the purpose of comparing *Phyllopodium palmatum* with other Australian cetoniines, we present generalized mating and stridulation behaviour observed for 23 Australian cetoniines. For males, we describe a pair of large genital brushes – a structure that has not been reported previously for Cetoniinae and that might be novel in Coleoptera as a whole. Modifications to the phallobase of several other Australian Schizorhinini are described.

Introduction

Flower chafers are important pollinators of various tree species but little else is known about their general biology (Cassis and Weir 2002, Hangay 2001). Detailed descriptions of courtship and mating behaviour have not been published for any species of Schizorhinini, Australia's largest tribe of Cetoniinae. This study reports the behaviour of *Phyllopodium palmatum* (Schaum, 1848) (Fig. 1) in the field (at Dunmore State Forest in Queensland) and of attempted matings by one pair under laboratory conditions. The species has been rarely collected but collection records and literature indicate a wide distribution from southeastern South Australia through Victoria and NSW to at least Cairns, Queensland, inhabiting coastal plains and the Great Dividing Range (Reid and Bulbert 2002). No ecological or behavioural information has been published previously on *P. palmatum* and the unique male genitalia have not been described before, although P. Hutchinson (pers. comm. 2010) recognized its unique structure and made a sketch of it.

Material and methods

Specimen collection, captivity and dissection

Seven specimens of *Phyllopodium palmatum* were collected in Dunmore State Forest (Table 1), using a net attached to a 12 meter Spiderbeam fibreglass pole (www.spiderbeam.com). Collections were made under Entomological Society of Queensland permit TWB/03/2012 issued to CHM.

All excursion and specimen codes refer to CHM's private collection (Microuniverse Cetoniinae Research Collection, Redland Bay, Qld, Australia, abbreviated as 'MIC' and listed in the Registry of Biological Repositories http://www.biorepositories.org). All specimens were collected in dry eucalypt woodland. The specific habitat of each collection site is shown in Table 2. Plants from which specimens were collected were identified by the Queensland Herbarium.
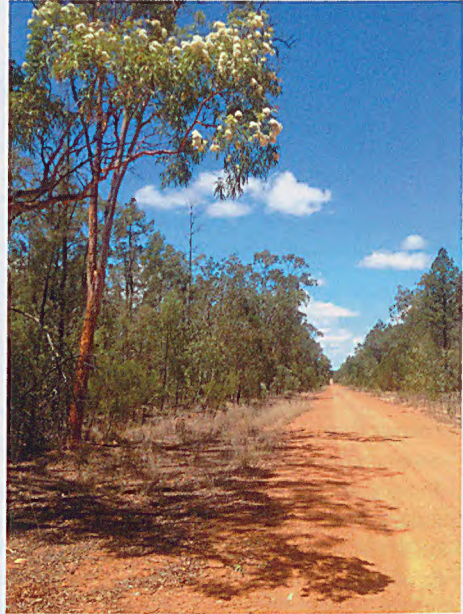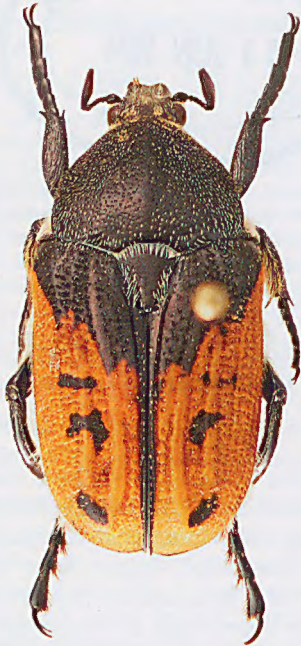
Figs 1-2. (1) Pinned adult male of *Phyllopodium palmatum*. Note difference in colour between the dead specimen here and live specimen depicted in Fig. 6. Image by Justin Bartlett, © DAFF 2013. (2) Typical habitat of *Phyllopodium palmatum*. *Angophora leiocarpa* (foreground) in bloom at Dunmore State Forest in December 2012.

Specimens were transported in coolers to Redland Bay, Qld for observation. Captive adults were kept in a transparent plastic rearing container 320 mm long, 210 mm wide and 100 mm deep, which had a mesh-covered hole for ventilation. The container was filled to a depth of approximately 4 cm with substrate consisting of decaying wood and humus collected at Redland Bay. Temperature and humidity in the container were kept ambient. The insects were offered banana slices, honey and a waterlogged tissue, each of which was replaced daily. Courtship and mating observations were made of one male and the female from Fire Tower 2 (MIC60967) that took place in a

Table 1. Collection localities of *Pyllopodium palmatum* used in this study, all in Dunmore State Forest, Qld, Australia. Geographic coordinates use datum WGS84.

Location	Latitude Longitude	Date	Collectors	Specimens collected with MIC specimen numbers	Host plant
Fire tower 2	-27.6267 151.0202	8.i.2011	C. & T. Moeseneder & C. Dale	3 males (MIC60967-001, MIC60967-005, MIC60967-023), 1 female (MIC60967-024)	*Angophora costata*
The Quarry	-27.6477 151.0279	8.i.2011	C. & T. Moeseneder & C. Dale	1 male (MIC60968-002)	
Tara Road junction	-27.7012 151.0322	4.xii.2012	C. & S. Moeseneder	1 male (MIC61062-001)	*Angophora leiocarpa*
Roadside	-27.61591 151.04809	21.xii.2013	C. & S. Moeseneder	1 female (MIC61144-001)	*Angophora floribunda*

Table 2. Regional ecosystem classifications at the collection locations, as per Regional Ecosystem Description Database (Queensland Herbarium 2013). DBVG = Dominant Broad-Scale Vegetation Group.

Location	DBVG	Description
Fire tower 2	11.5.4	*Eucalyptus crebra* F.Muell., *Callitris glaucophylla* Joy Thomps. & L.A.S.Johnson, *C. endlicheri* (Parl.) F.M.Bailey, *E. chloroclada* (Blakely) L.A.S.Johnson & K.D.Hill, *Angophora leiocarpa* (L.A.S.Johnson ex G.J.Leach) K.R.Thiele & Ladiges on Cenozoic sand plains/remnant surfaces. Deep sands.
	11.7.4	*E. decorticans* (F.M.Bailey) Maiden and/or *E.* spp, *Corymbia* spp, *Acacia* spp, *Lysicarpus angustifolius*(Hook.) Druce on Cenozoic lateritic duricrust.
The Quarry	11.5.4	*E. crebra*, *Callitris glaucophylla*, *C. endlicheri*, *E. chloroclada*, *Angophora leiocarpa* on Cenozoic sand plains/remnant surfaces. Deep sands.
Tara Road junction	11.3.14	*E.* spp., *Angophora* spp, *Callitris* spp. woodland on alluvial plains.
	11.3.25	*E. tereticornis* Sm. or *E. camaldulensis* Dehnh. woodland fringing drainage lines.

rearing container. After termination of observations, all specimens were killed in 100% ethanol and dry-mounted. Male genitalia were removed and preserved after examination.

Audio and video

Video recordings were made of stridulation and other behaviour using an Apple iPad 2 and uploaded to http://www.nature.cc/palmatum/index.html. A contents page at this location lists the available videos. Those relevant to this publication are for disturbance stridulation: http://nature.cc/palmatum/ Phyllopodium_palmatum_064.MOV   and   http://nature.cc/palmatum/ Phyllopodium_palmatum_085.MOV; and for stridulation simulation: http:// nature.cc/palmatum/Phyllopodium_palmatum_090.MOV. Additional videos may be uploaded in the future.

All video files are available under Creative Commons license of Attribution-Share Alike 3.0 Unsupported (CC BY-SA 3.0). Pazera Free Audio Extractor 1.4 was used for audio extraction. Audacity 2.0.2 was used for visualization and to remove background noise by sampling a section which did not contain stridulation sound, creating a noise profile from it and using the profile with the noise removal command. Playback of stridulation was through an Apple iPad 2.

Results/Observations

Cohort

In Dunmore State Forest in 2011 and 2012, *P. palmatum* was collected in the vegetation communities listed in Table 2, with 10 other cetoniines, on flowering trees (*Angophora costata* (Gaertn.) Britten, *Angophora leiocarpa* (Fig. 2) and *Angophora floribunda* (Sm.) Sweet), *Chlorobapta frontalis* (Donovan *et al.*, 1805), *Clithria albersi* Kraatz, 1885, *Clithiria eucnemis* (Burmeister, 1842), *Dilochrosis atripennis* (Macleay, 1863), *Glycyphana (Glycyphaniola) brunnipes* (Kirby, 1818), *Glycyphana (Glycyphaniola) stolata*, *Microvalgus* Kraatz, 1883 sp., *Neorrhina octopunctatum* (Burmeister, 1842), *Neorrhina punctatum* (Donovan *et al.*, 1805) and *Schizorhina atropunctata* (Kirby, 1818).

Genital brushes

The aedeagus of males of *P. palmatum* (Fig. 3A) possesses a pair of large genital sclerites, here called "genital brushes". The brushes originate from the ventral region of the *pars basalis* and protrude slightly beyond the extended parameres. Each bears several rows of long, dense setae that are progressively longer from the base of the sclerite towards its apex. Two actions of the brushes were discernible: 1) when the parameres were extended before copulation, by rotation through approximately 90 degrees, the setae of each sclerite moved across the distal face of the parameres and when the parameres were retracted after copulation the setae of each sclerite moved

across the proximal face of the parameres; 2) the genital brushes were pushed aside by the edge of the female's pygidium as the parameres entered the female and therefore remained outside the female. This could be observed since the soil was shallow in some areas of the container. The brushes are compact despite their size and allow the aedeagus to stay in a tight unit (Fig. 3A, ventral view).
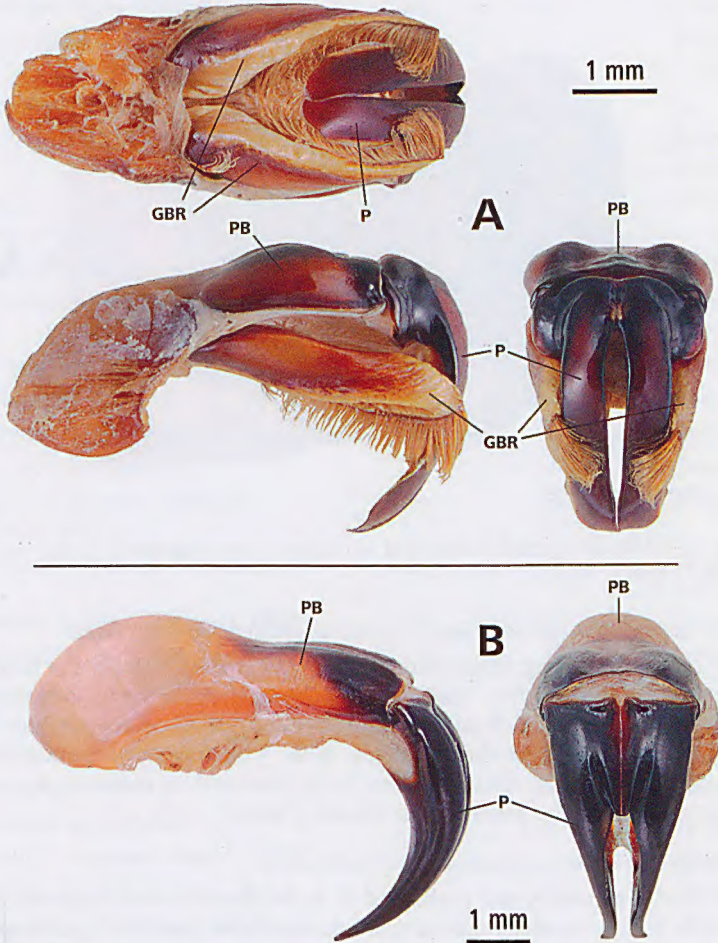

Fig. 3. Comparison of aedeagi: (A) *Phyllopodium palmatum*; (B) *Chondropyga dorsalis*. GBR = genital brushes, P = parameres, PB = *pars basalis*. Note difference in scale: *C. dorsalis* images are shown approximately 25% smaller than *P. palmatum*. Images by Justin Bartlett, © DAFF 2013.

When other Australian Schizorhinini were inspected, further modifications of genital sclerites were found. The ventral surface of the *pars basalis* of *Neoclithria eburneoguttata* (Blanchard, 1850) (Fig. 4) bears two small, setose sclerites. In *Trichaulax macleayi*, *T. marginipennis* and *T. nortoni* (Butler, 1865) the ventrolateral area of the *pars basalis* is expanded to form a lamella. In *Metallesthes metallescens* (White, 1859), another Australian Schizorhinini, the ventral surface of the phallobase bears a rectangular, sclerotised patch.
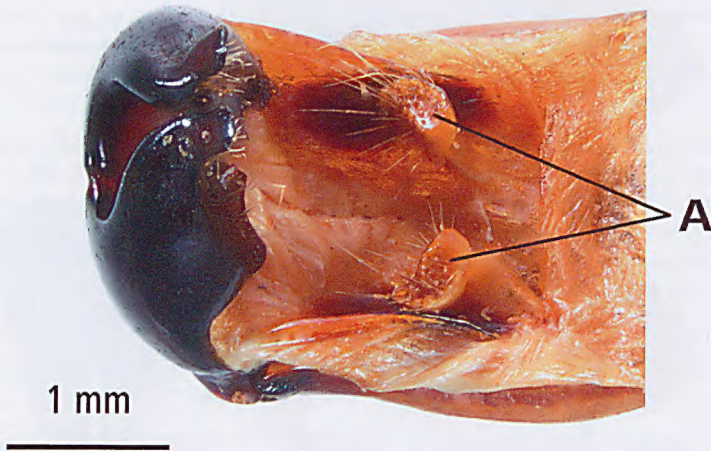

Fig. 4. A–Additional genital sclerites in *Neoclithria eburneoguttata*. Image by Justin Bartlett, © DAFF 2014.

Courtship and mating behaviour of selected Australian Cetoniinae

In this study and during observations made over several years in the field and under rearing conditions, other Australian cetoniines were observed to copulate following little or no courtship (Table 3). In these species, the usual mating location is where the two sexes meet – on flowers. However, when given the opportunity, these species were observed to mate in any other location such as on the ground or in breeding boxes.

Courtship and mating behaviour of P. palmatum

In this study, courtship and mating of *P. palmatum* was not observed in the field. The following observations were made of one pair of *P. palmatum* in captivity in a breeding container (as described in Methods), where the beetles were initially placed so that the female would oviposit in the soil. When the male mounted the female it used its broad, flat protarsi and metatarsi to tightly clasp the female. The male produced a sound consisting of two to approximately five pulses and also clasped the female tightly with its

Table 3. Mating and courtship in Australian Cetoniinae, excluding *P. palmatum*. All observations by CHM, except those with footnotes. n. obs.= not observed.

Species	Stroking	Stridulation	Usual place of copulation
Cetoniini			
Glycyphana (Glycyphaniola) brunnipes	n. obs.	no	n. obs.
Glycyphana (Glycyphaniola) stolata	no	no	flowers
Protaetia fusca	no	no	flowers, tall grass?
Schizorhinini			
Chondropyga dorsalis	no	no	flowers, ground
Chlorobapta frontalis [1]	yes	no	flowers
Clithria albersi	n. obs.	no	n. obs.
Clithria eucnemis	n. obs.	no	n. obs.
Dilochrosis balteata (Vollenhoven, 1871)	no	no	flowers, fruit?
Dilochrosis walteri Lea, 1914	no	no	flowers
Dilochrosis atripennis	no	no	flowers
Dilochrosis brownii (Kirby, 1818)	no	no	flowers
Eupoecila australasiae	no	no	flowers
Hemipharis insularis (Gory and Percheron, 1833)	no	no	flowers
Ischiopsopha wallacei (Thomson, 1857)	no	no	flowers, masses [3]
Lyraphora velutina (Macleayi, 1863)	no	no	flowers
Lyraphora obliquata (Westwood, 1842)	no	no	flowers
Mycterophallus duboulayi (Thomson, 1878)	no	no	flowers
Neorrhina octopunctatum	n. obs.	no	n. obs.
Neorrhina punctatum	no	no	flowers
Schizorhina atropunctata	no	no	flowers
Trichaulax concinna (Janson, 1873) [2]	yes	no	flowers
Trichaulax macleayi Kraatz, 1894 [2]	yes	no	flowers
Trichaulax marginipennis (Macleay, 1863) [2]	yes	no	flowers

[1]Observation by R. Zietek (pers. comm. 2013). [2]Observations by J. Hasenpusch (pers. comm. 2013). [3]This species is known to occur in great masses which hang on host trees. Mating consequently occurs within these masses.

strongly bent metafemora and metatibiae. Over several minutes, the male then performed 1-2 second-long, rapid body movements and stridulation sequences and moved its shortened mesolegs sideways against the female. The sound-producing structures are shown in Fig. 5. Frequently, the female also stridulated, showed a general increase in activity and performed rapid, sideways shaking movements. The female became very active with each putative stimulation sequence. Copulation was observed three times in the same pair. In approximately 75% of the attempts the female shook off the male and copulation was not achieved. In those cases where the outcome was copulation, about one to three minutes into the assumed courtship display, the female began to bury into the substrate in the breeding container while the male continued to clasp her. Copulation commenced in the soil, never above ground. The latest observations were made at 2300 h, with artificial light, by which time the activity of the beetles had not diminished. Adult males and the female often fed on banana slices when they were not engaged in mating.
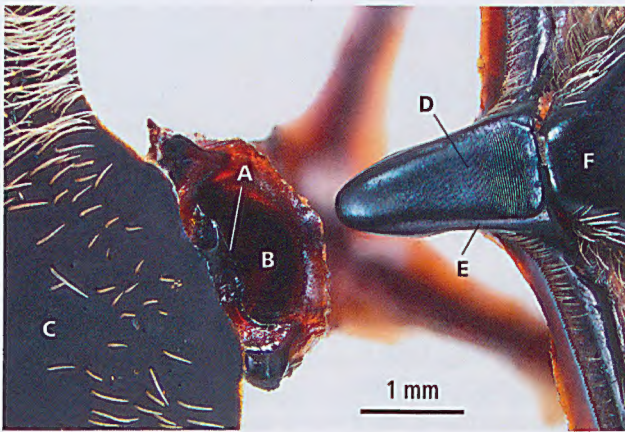

Fig. 5. Stridulation sound production structures in *P. palmatum*. A = plectrum, B = cavity in apex of metasternum, C = metasternum, D = file, E = process of first abdominal segment, F = first sternite. Metasternum is held at an angle of 45° to increase visibility of the plectrum. In vivo, the process enters the cavity on the same plane. Image by Justin Bartlett, © DAFF 2014.

Defensive behaviour

Phyllopdium palmatum appears to have several types of defensive behaviour. When a hand was brought near the mating pair of *P. palmatum*, they immediately stridulated and raised and spread their metalegs (Fig. 6). Raised metalegs as a reaction to disturbance was also observed in *Trichaulax philipsii* (Schreibers, 1802) by CHM.

Fig. 6. Male of *Phyllopodium palmatum.* Putative defensive posture, with raised metalegs, evoked by disturbance.

Stridulation

In addition to stridulation during courtship, both males and females of *P. palmatum* stridulated when disturbed but never spontaneously. Each time the observer moved a hand close to a specimen, the beetle performed a jerking movement and emitted a few stridulating pulses. When beetles of either sex were held by the observer, they initially stridulated constantly (here called a *disturbance stridulation sequence*) (see videos described in Methods) with 29.8 impulses measured in 5.14 seconds, indicating 5.79 impulses per second (Fig. 7). Within several minutes of handling, the beetles stridulated increasingly less often until only increased disturbance provoked a response. A recording of a disturbance stridulation sequence was played back to another male, which showed no observable reaction to the sound.

Stridulation in both sexes was found to be produced by metasternal-sternital means in *P. palmatum*. A process in the middle of the base of the first abdominal sternite (Fig. 5E) is taken up by a recess in the centre of the hind margin of the metasternum between the hind coxae (Fig. 5B). In *P. palmatum*, the process of the first sternite is flat, broad and its ventral surface bears approximately 150 transverse striations (Fig. 5D), providing the function of a file. The metasternal cavity bears a sharp, straight, transverse cuticular ridge, which functions as a plectrum (Fig. 5A). The beetle stridulates by rapidly moving the abdomen and thereby scraping plectrum and file against each other. This method of stridulation was easily seen on living beetles when they were held upside-down and was documented (see

videos described in Methods). When the dissected parts were held and moved in the same manner, we were able to produce a similar stridulation sound (see video described in Methods). The Australian cetoniines *E. australasiae* and *C. dorsalis* were examined and, while they were found to have the same general structure of the process of the first sternite and the recess of the metasternum, they did not have the plectrum and file modifications and did not produce sound.
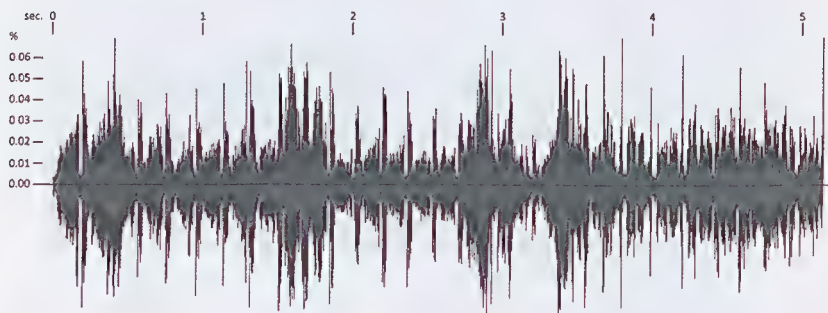

Fig. 7. Oscillogram of stridulation sequence of male of *Phyllopodium palmatum* evoked by disturbance. Horizontal axis = time in seconds, vertical axis = percent of allowable volume.

Additional observations

Male *P. palmatum* were found to have two-pointed inner mesoclaws and rainbow-coloured reflections in some black dorsal areas. Extremes of elytral coloration ranged from reduction of black to base of elytra and two very small macula on each elytron, to melanic with entirely black elytra except for lateral and apical areas (both in collection of Jack Hasenpusch, Australian Insect Farm, Innisfail, Qld).

Discussion

Courtship and mating

In many Australian Schizorhinini, antennal clubs of males and females are approximately the same size, presumably since the sexes encounter each other on flowers and require less specialized structures such as enlarged antennal clubs in males (Hutchinson and Moeseneder 2013) to locate females. This is the case for the cohort of 10 species with which *P. palmatum* was found at Dunmore S.F (Table 3). It is likely that males and females of *P. palmatum* meet on flowers since the antennal clubs of both sexes are of similar size.

Copulation in *P. palmatum* appears to occur only after a sequence of putative courtship behaviour has taken place. In this study, the courtship behaviour appeared to be comprised of stridulation, increased movement, stroking with legs, shaking and burying. This specific combination of behaviour was not seen in the 23 other Australian Schizorhinini for which observations are reported (Table 3) and it appears to be considerably more complex and to consist of more elements than previous observations of other species indicate.

Predation and defence

Several aspects of the unique morphology and behaviour of *P. palmatum* could be the result of high predation from birds, as observed in *Eupoecila australasiae* (Donovan, 1805) and *Chondropyga dorsalis* (Donovan, 1805) by Alderson (1976). Stridulation, which was observed for this species when disturbed and in courtship, has been shown to repel predators in several experiments, such as with mutillid wasps, water scavenger beetles and round sand beetles (Masters 1979). The putative defensive posture with raised metalegs that the beetles assumed upon disturbance (Fig. 6) is most likely a threat display against predators. *Trichaulax philipsii* was observed (by CHM) to react in the same way to disturbance and P. Hutchinson (pers. comm. 2013) reported that *Dilochrosis walteri* reacted to the sound of a camera's shutter with the same posture. He also noted that *D. walteri* uses the same movement of the metalegs to right itself from an inverted position.

Stridulation

The stridulation sound in adult *P. palmatum* is produced by metasternal-sternital means and is therefore different than those methods described for Australian cetoniines and Australian Scarabaeidae in general.

Production of sound in adult cetoniines has been rarely described in scientific literature (Wessel 2006) but it appears to be more common than the literature reveals (personal communication by CHM with cetoniine workers). For example, P. Malec (pers. comm. 2012) observed stridulation in adults of the goliathine *Tmesorrhina simillima* Kraatz, 1880 and J. Maté (pers. comm. 2012) observed stridulation in adults of the cetoniines *Protaetia* (*Netocia*) *morio* (Fabricius, 1781) and *Tropinota squalida* (Scopoli, 1783). According to Wessel (2006), sound in adult Cetoniinae is produced in elytro-abdominal and abdomino-femoral regions. Within the Schizorhinini, stridulation has been reported from *Ischiopsopha* Gestro, 1874, where the sound is produced in the abdomino-tibial (not abdomino-femoral) region. Sharp (1874) described stridulation in three species of adult *Ischiopsopha* (all in *Lomaptera* Gory & Percheron, 1833 at that time) produced by a series of fine ridges on the third and fourth abdominal segments (erroneously identified as the second and third segments) and on the inside of the metatibia. This has been verified by inspection of *I. bifasciata* (Quoy & Gaimard, 1824) in the MIC collection; the same structures were found on the Papua New Guinean

species *I. jamesi* (Waterhouse, 1876) and *I. lucivorax* (Kraatz, 1890) and the Australian species *I. wallacei* (Thomson, 1857) and *I. pulchripes* (Thomson, 1877).

Genital brushes

We reviewed the genitalia of 1104 species (32% of approximately 3395 species: Krajcik 1998, 1999) of Cetoniinae from all tribes except Stenotarsiini and Diplognathini in literature and in the MIC collection. None has a structure similar to the genital brushes found in *P. palmatum*.

In Coleoptera, sclerites of the aedeagus in addition to the phallobase and parameres are known in few species. Some of these structures of the aedeagus may function as true brushes, such as that described by Arnaud *et al.* (2001) in the tenebrionid *Tribolium castaneum* (Herbst, 1797). In this species, a brush-like organ which is embedded centrally in the aedeagus is used in removing pre-existing sperm from a female's reproductive tract (Arnaud *et al.* 2001). Özdemir (2008) described two species of *Dermestes* Linnaeus, 1758 that bear a row of long setae on the parameres that have the appearance of brushes, but these are not attached to novel structures. Li *et al.* (2008) described armature of the internal sac of the parameres in seven species of *Epitrichius* Tagawa (in the cetoniine tribe Trichiini). The armature consists of a minor and a major hook and is located in the internal sac, a short distance from where the brushes of *P. palmatum* originate. No specific purpose of the armature was described.

We observed modifications to the sclerites of the ventral area of the phallobase in six Australian Schizorhinini. Three species bear additional sclerites; three have modifications to existing sclerites. The most similar structures to those found in *P. palmatum* are in *Neoclithria eburneoguttata*, a species that otherwise bears little resemblance to *P. palmatum*. In this species, two small, rounded and setose sclerites (Fig. 4) originate a short distance apically from where the brushes in *P. palmatum* are attached on the *pars basalis*. While they are too short to perform the functions we described for *P. palmatum*, they could be homologous, before complete development or residual after the loss of such, to the fully developed brushes of *P. palmatum*.

Our observations suggest that the genital brushes in *P. palmatum* males have a role in the cleaning of male and female copulatory parts during mating in soil since the brushes are spread laterally upon copulation and move across the apical edge of the female's pygidium. However, since numerous other Coleoptera species (for example geotrupines and aphodiines) are known to mate in substrate such as wood and soil that could interfere with the function of copulatory structures but have not developed genital brushes with cleaning functions, it is possible that the brushes may be used in the stimulation of the female pygidium, to remove pre-existing sperm from the female or for entirely other functions.

Production of novel structures, such as the brushes of *P. palmatum*, likely comes at a cost (Daly 1978). Nijhout and Emlen (1998) showed that trade-off in allocation of shared resources can occur during the developmental growth of body parts – if one part uses more resources, another near it receives less, for example in horns of scarabs. Such a compensatory response might account for the fact that the parameres of *P. palmatum* are only approximately 75% as large as those of *C. dorsalis* and *C. gulosa* (Janson, 1873) (Fig. 3b), despite the beetles being about the same overall size. Furthermore, it is very unusual for such large, complex structures as the brushes to develop through evolution without modification or duplication of existing structures.

Conclusion

Phyllopodium palmatum appears to have more complex courtship behaviour than other Australian cetoniines. Further standardized observations in natural circumstances are needed to determine whether the observed behaviour of *P. palmatum* is repeated in the field. Males possess a very unusual and novel structure compared with other members of the subfamily and other beetles in general. Some comparative morphological studies, based on well-supported phylogenies, are required to understand the origins of these genital brushes and further observations may prove whether the function of the brushes is linked with its reproductive behaviour. Modifications to the phallobase exist in other Australian Schizorhinini, indicating an area of study in future morphological work.

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